DISTRIBUTION, AFFINITIES AND ORIGIN OF THE PUNCIIDAE (CRUSTACEA: OSTRACODA)

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The punciid ostracod has, since its discovery been recognised as a probable living representative of the Palaeozoic Kirkbyacea. Similarities in larval development of the carapace are discussed including a comparison of the manawan nauplius with an unusual Ordovician 'larva' *Melopetasus*. Internal structure, reticulation, muscle scars, ornamentation and the frill of the punciid carapace more closely resemble the kirkbyid pattern than that considered typical for modern, extant, podocopid ostracods. The anatomy of the punciid trunk displays remarkable similarity posteriorly to that found on the extant platycopid *Cytherella*. This condition is considered plesiomorphic for ostracods. ☐ *Crustacea, Ostracoda, Kirkbyacea, Punciidae, Palaeozoic/Recent, carapace morphology, soft anatomy, homologies.*

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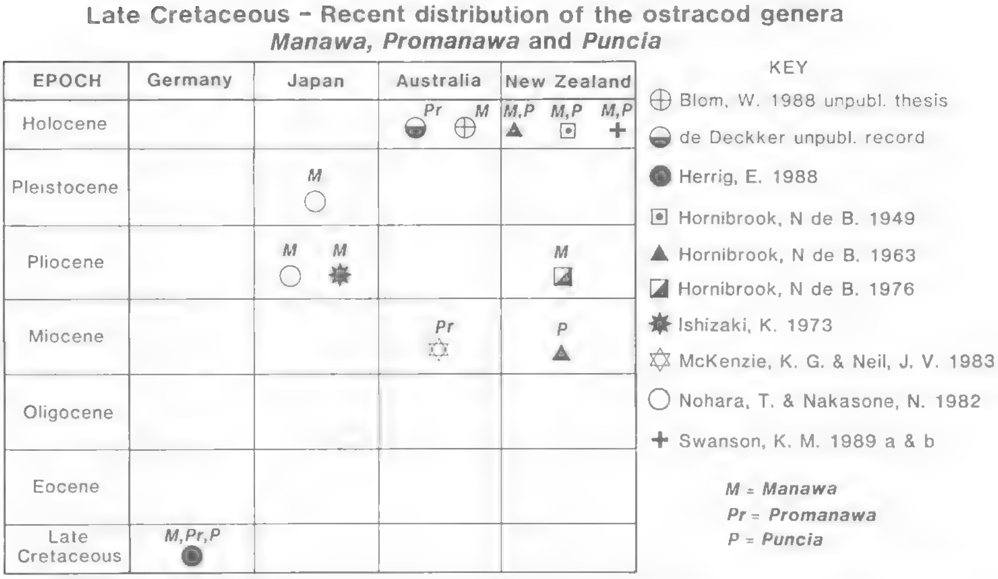
The recent recovery of rare, live specimens of the punciid ostracod *Manawa staceyi* has led to a dramatically improved, though incomplete, understanding of the anatomical and ontogenetic peculiarities of the Punciidae (Swanson, 1989a, b). Specimens of the remaining punciid genera *Promanawa* and especially *Puncia* also occur rarely, in both cases however, only disarticulated valves have been found. From the time of its initial discovery (Hornibrook, 1949) *Puncia* has been recognised as an animal whose biology, once documented, could have profound effects in areas much broader than the discipline of ostracodology from whence such data was generated.

Although '..reluctant to assert that a representative of a group of ostracods, which apparently died out elsewhere in the Devonian (400 MYBP), is still living in the South Pacific', Hornibrook (1949) established (a) that both *Puncia* and *Manawa* were unlike any other known living ostracod, and (b) *Puncia* most closely resembled members of the Palaeozoic (Lower Ordovician – Upper Devonian) ostracod family Eurychilinidae. Later, after a more detailed reexamination of the 1949 specimens and additional fossil material of *Puncia* from the Miocene (20 MYBP) of New Zealand, he concluded 'The only feasible conclusion is to regard the Punciidae as a relict group of Paleocopida, which were the dominant order of ostracodes in the Palaeozoic' (Hornibrook, 1963).

It is not the purpose of this paper to document historically the development of punciid classification since that time, such interests are adequately accommodated elsewhere (Swanson, 1989a). It should be noted however, that the dolonic dimorphism displayed by a number of eurychilinids is not found in the frill of *Puncia* (Swanson, 1985). Additionally the 'lunettes' of *Manawa* which Hornibrook felt may indicate a brooding capability, are now considered a simple, economic form of buttressing between the carapace proper and its sole (Swanson, 1989a). In most sexually dimorphic podocopid ostracods, males and females may be distinguished by variations in carapace shape and size; Nohara and Nakasone (1982), after examining a number of valves of *Manawa konishii*, considered equivalent differences also occur in the punciids.

In many respects, the release of some anatomical and ontogenetic details for *Manawa staceyi* (Swanson, 1989b) created more difficulties than were solved. At least three instars carry a single, horizontal, shield-like carapace; a feature hitherto unrecorded for ostracods. Although the adults are bivalved, each valve is extended laterally during ambulatory excursions presenting an exaggerated gape. This contrasts sharply with a vertical stance and 15 – 20° gape (Benson, 1981) for 'normal' ostracods. Anatomically, *Manawa staceyi* possesses a segmented abdomen and paired furcaxlamellae; metanaupliar development witnesses the addition of four pairs of homonomous, thoracic legs, the anterior – most progressively assuming a locomotory/trophic role. Cephalisation, however, remains incomplete at maturity. Since the appearance of



Late Cretaceous - Recent distribution of the ostracod genera *Manawa, Promanawa* and *Puncia*

EPOCH	Germany	Japan	Australia	New Zealand
Holocene			*Pr* ⊖ *M* ⊕	*M,P* ▲ *M,P* ⊡ *M,P* +
Pleistocene		*M* ○		
Pliocene		*M* ○ *M* ✸		*M* ◪
Miocene			*Pr* ✡	*P* ▲
Oligocene				
Eocene				
Late Cretaceous	*M,Pr,P* ●			

KEY
⊕ Blom, W. 1988 unpubl. thesis
⊖ de Deckker unpubl. record
● Herrig, E. 1988
⊡ Hornibrook, N de B. 1949
▲ Hornibrook, N de B. 1963
◪ Hornibrook, N de B. 1976
✸ Ishizaki, K. 1973
✡ McKenzie, K. G. & Neil, J. V. 1983
○ Nohara, T. & Nakasone, N. 1982
+ Swanson, K. M. 1989 a & b

M = Manawa
Pr = Promanawa
P = Puncia

FIG. 1. Upper Cretaceous – Recent distribution of the ostracod genera *Manawa*, *Promanawa* and *Puncia*.

the 1989 papers I have become aware of other work (Fig. 1) which in retrospect adds considerably to the discussion of some 'manawan novelties'. Conversations with a number of Palaeozoic ostracod researchers at the 1989 'European Ostracodologists' Meeting' in Frankfurt and progress in my own investigation of platycopid and polycopid ontogeny now mean that sufficient new data are available to warrant a reassessment of the punciid ostracod and its relationship to other crustaceans.

THE PUNCIID CARAPACE

LARVAE

As previously stated, the single, dome-shaped carapace carried by the nauplius of *Manawa staceyi* (Figs 3D, E) is unique for ostracods and possibly for Crustacea. Phaselus larvae, first described from the Ordovician (500–400 MYBP) of Spitsbergen by Fortey and Morris (1978), were considered by those authors to be the remains of 'nauplius-like' trilobite larvae. Schram (1982) disputed this claim, including in his reasoning the fact that a doublure is not unique to trilobites (the presence of a doublure on phaselus larva was seen by Fortey and Morris as a key indicator that such remains were trilobitan). By definition (Harrington, *et al.*, 1959) the earlier described carapace sole (Swanson, 1989b) of *Manawa* also qualifies as a doublure. Schallreuter (1979) considered similar remains from Upper Ordovician erratics on the Isle of Sylt as representing 'an ontogenetical stage of a bilateral-symmetrical animal (? trilobite).' Significantly, a smaller larval form (*Melopetasus*), which displays quite remarkable similarities to the carapace of the manawan nauplius, was also isolated (compare Fig 3D, E, G, H). The weight of evidence, I believe, favours acceptance of the Ordovician dome-shaped larvae as punciid-like (or at least ostracodal) rather than trilobitan. One must acknowledge that the position of the phaselus (a bilaterally symmetrical body created by the folding of a dome along a 'dorsal' axis) in this scenario is problematic. In *Manawa staceyi*, during the transition from nauplius to metanauplius, the naupliar dome occasionally shows evidence of slight infolding (Fig. 3D); examples of the exaggerated phaselus-type fold, however, have never been recovered from modern sediments. Either the phaselus is unrelated to the manawan-type naupliar dome (favoured by this author) or it may represent an additional larval stage which has subsequently been eliminated from the 'punciid' ontogeny.

In the Cambrian (520 MYBP), phosphatocopine bivalvedness (exhibited by *Hesslandona unisulcata*) is achieved by the folding of the carapace along a dorsal mid-line (Müller,1982). This contrasts with modern podocopid ostracods in which an array of complex hinge structures develop around a dorsal, mid-line suture (see Swanson, 1990). It is most likely that the plesiomorphic crustacean naupliar condition occurs within a variety of forms described from the Upper Cambrian of Sweden (Müller and Walossek, 1986, 1988; Walossek and Müller, 1989). In fact, as indicated by those authors, the Cambrian larval types A and B are remarkably similar to the free-living naupliar groundplan exhibited by a number of extant crustaceans. To date no equivalent of the manawan naupliar dome has been recorded from the Cambrian, acknowledging the possibility that such remains are overlooked simply because they are so unfamiliar.

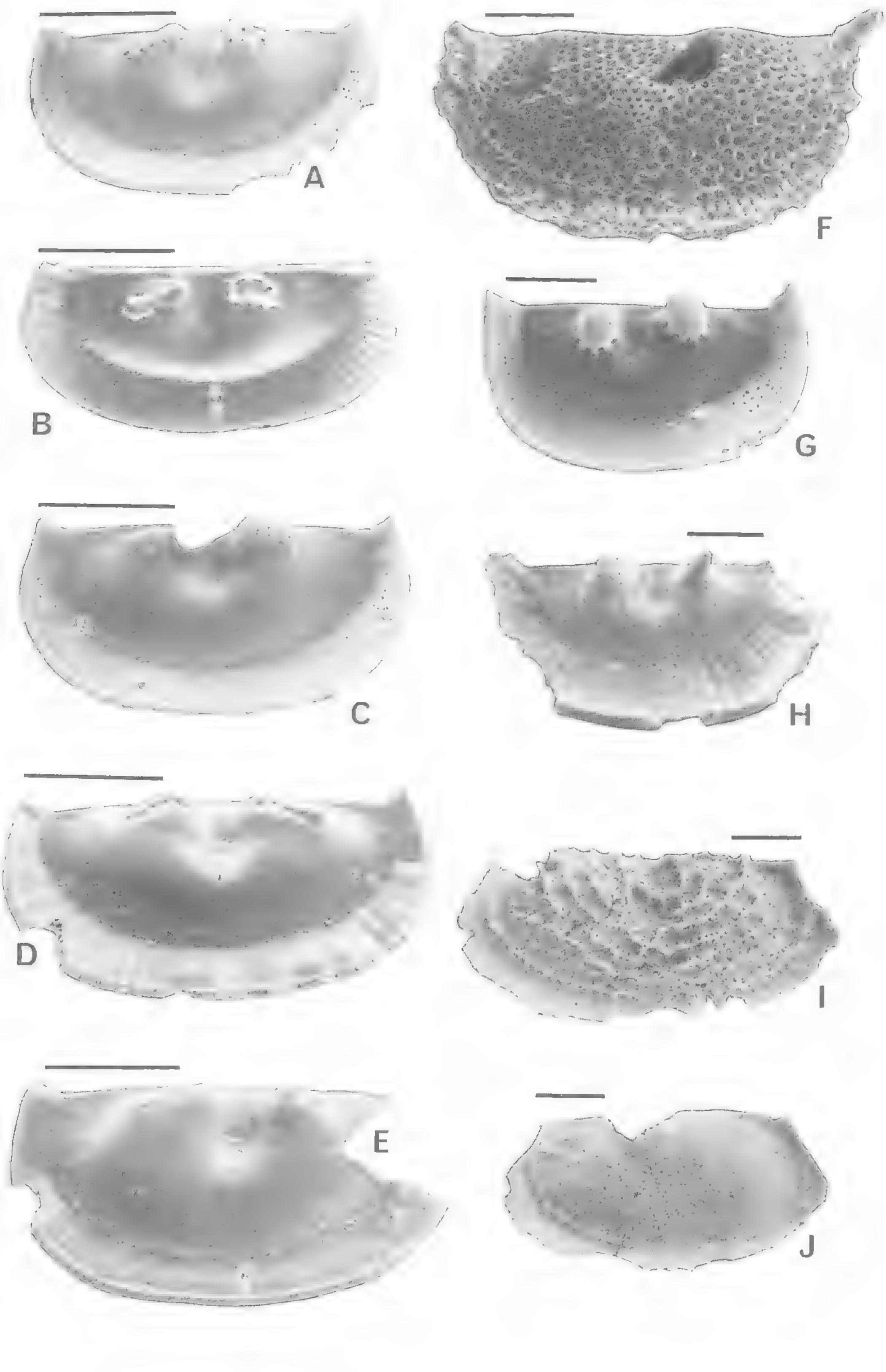
Extant species of *Manawa* occur in shallow, high-energy, marine environments; as a consequence one is led to speculate that the development of a relatively heavy naupliar carapace, although offering protection, also locked such larvae into a non or poorly dispersive, benthic mode. The fact that nauplius larvae are recovered in reasonable numbers with the adults suggests the eggs also remain quite localised during development (there is to date no evidence of brooding); no podocopid ostracods, as far as I am aware, utilise a saturation method of egg production/fertilisation to promote dispersal into the plankton. Perhaps therefore we should, as Hornibrook suggested, consider the punciids as relict, a shadow of their former selves, the Kirkbyacea – the assumed ancestral stock of the Punciacea (Swanson, 1989a) – whose more recent (15 MY - present day) distribution (Fig. 1) in a series of isolated, widely-distributed pockets is the remains of a diversive/dispersive event which climaxed some three to four hundred million years ago.

Muscle Scars

In ostracod taxonomy, muscle scars are an extremely useful tool. Most specimens (fossil and living) of punciid ostracods display a full complement of well-preserved scars; in contrast, representatives of the Palaeozoic Kirkbyacea, although nearly always presenting the characteristic 'kirkbyan pit' externally, more often than not have the internal muscle scar detail obliterated as a result of imperfect preservation (G. Becker, pers. comm.). In his description of the central muscle scar field of one group of kirkbyaceans, Sohn (1954) concluded '...even the best preserved specimens show only one knob on the inside of the valve without any trace of areas of attachment of accessory muscles'. Results of a recent re-examination of a number of Sohn's types indicate a variety of muscle scar types as diverse as that expected for 'modern' podocopid ostracods. The complete muscle scar pattern for punciids was first described by McKenzie and Neil (1983) from the carapace of a new genus *Promanawa*. It consists of a central adductor group of six scars arranged biserially, two dorsal scars (the larger occurring on an elevated node) and a single mandibular scar. Frontal scars were considered absent. Such a pattern, they concluded, indicated the punciids were benthic crawlers with a mandibular coxale capable of a transverse biting action (Swanson, 1989b). The kirkbyid pattern, assuming *Aurikirkbya wordensis* (Hamilton, 1942) is representative, also possesses two dorsal scars and a weakly developed mandibular scar (Becker, 1989). In contrast however, the central adductor area consists of an undifferentiated node and a frontal scar is also present. Becker (1989) concluded that this species was probably a nectobenthic filter-feeder. Ostracods generally exhibit a variety of often quite complex central muscle scar patterns. Thus, it seems probable that an apparent lack of differentiation in the kirkbyid node reflects imperfect preservation rather than some anatomical peculiarity. Contrasts in the central muscle scar fields, as they are presently understood, cannot therefore be used reliably as evidence against a kirkbyacean-punciacean continuum. Additionally, as noted by McKenzie and Neil (1983), *Promanawa australiensis* does have a well developed 'kirkbyid pit' externally; other members of the Punciidae do not, presumably because they have a much weaker reticulum

Frill

'The punciid selvage is at least an analogue of the velar ridge in Beyrichicopida and might well be homologous with it' (McKenzie and Neil, 1983). This is not supported by my work on *Manawa* which indicates that the ventral lunettes are structurally and functionally (?) quite distinct. From the outset, discussion on the relationship between the extant Punciidae and a possible Palaeozoic predecessor has invariably been dominated by the presence/absence of homologous structures in the frill. 'In summary, then, I see no objective basis to separate *Puncia* and *Manawa* from the Palaeozoic Beyrichiidae, which as I understand them include Palaeozoic straight-backed ostracods, with both cardinal angles well defined; a marginal frill typically extends adjacent to the free margins from cardinal angle to cardinal angle; the frill is doubly walled and has inner partitions corresponding to exter-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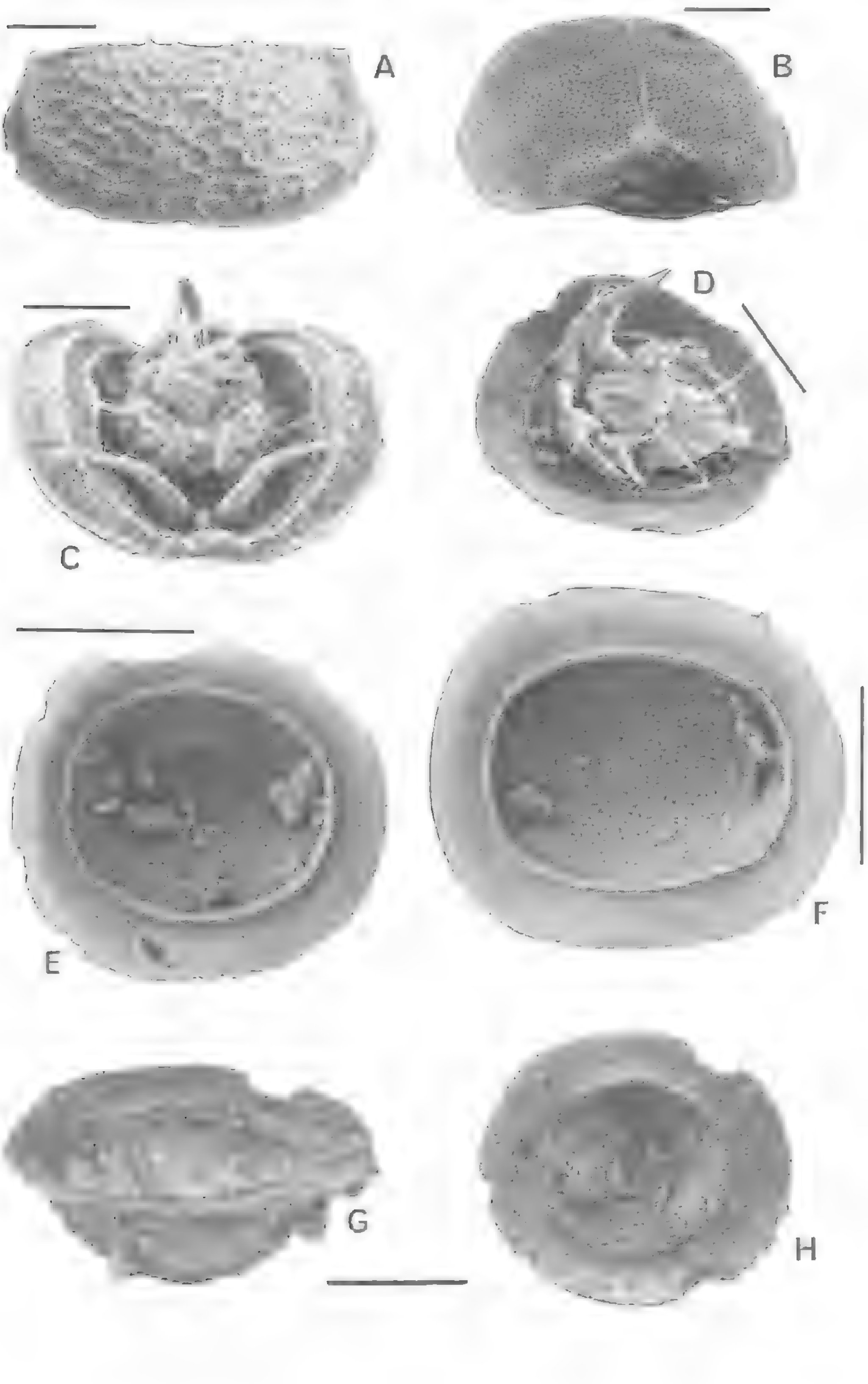
nal radial striae; in general, dimorphic pouches are formed by swelling of the frill, but such pouches are unknown in several early, primitive genera' (pers. comm. from F.M. Swartz to N. de B. Hornibrook). In most respects our assessment of the Palaeozoic ostracod frill remains unchanged, acknowledging that 'the ability of forming adventral extensions has been acquired independently in different, remotely related groups of Palaeocopa' (Jaanusson, 1957). With the availability of modern analogues/homologues (*Puncia and Promanawa*), it is now possible to compare and contrast this unique structure in detail. The total number of chambers in each frill is quite variable: 35 in *Coronakirkbya hamori,* (Kozur, 1985), noting the specimen is fragmented; 37–38? in *Coronakirkbya krejcigrafi*, fragmented; 31 in *Aurikirkbya* sp. A also fragmented (Becker, 1978); 55 in *Coronakirkbya fimbriata* (pers. comm. G. Becker). This pattern is repeated in the Punciacea: 28 in *Puncia goodwoodensis,* (Hornibrook, 1963); 40 in *Promanawa australiensis,* (McKenzie and Neil, 1983); 42 in *Puncia novaezealandica*, (Hornibrook, 1963); 43 in *Puncia* sp. A (Fig. 2E). In *Puncia* and *Promanawa* the septa which divide the frill into approximately 40 chambers are not radial pore canals (Swanson, 1985); additionally, access to the domicilium via these chambers is prevented by a thin, calcareous (?) wall or membrane (Fig. 4B). At the ventral edge of the frill, each chamber may be completely or only partially sealed, the latter resulting from incomplete calcification (Fig. 4B). A similar situation occurs in most Kirkbyacea, in the hollinacean *Oepikium* and in eurychilinids (Jaanusson, 1957), noting however that in these Palaeozoic taxa most chambers are circular/ovoid in section rather than rectangular. Although some specimens give an indication that the kirkbyid frill is composed of a row of distinct tubules, I suspect that this is an artefact of preservation/extraction and that in life the gaps between individual chambers were closed by a thin calcareous bridge. Ventral chamber exits, where present, were also extremely small since in many instances the ventral extremity of the calcareous bridge is tapered to a fine edge (Becker, 1978, pl.3, figs 17a–c, 18b). Determination of the function of the frill must await the discovery of living specimens of *Puncia* or *Promanawa*, however the possibility that these structures performed a dual role as both benthic support and gas-filled floatation-aid cannot be excluded. Adamczak (pers. comm.) has also found some form of membraneous (?) closure in the crumen of the Ordovician genus *Craspedobolbina*; this he felt could indicate a ballast/brooding function for that structure. Although McKenzie and Neil (1983) suggested the punciid frill did not appear till quite late in ontogeny ('until after the development of the anlages of reproductive characters in the soft anatomy'), evidence from imperfect ontogenetic sequences for *Puncia* (Fig 2A – E), *Aurikirkbya* and *Coronakirkbya* (Becker, 1978, pls. 3, 4) indicate that it is carried by 'early' juvenile stages as well.

PORES AND SETAE

Marginal pore canals with their associated setae, as found in most podocopid ostracods, do not occur within the Punciidae. Okada (1982) observed that in some taxa (*Bicornucythere bisanensis*) 'no pore runs along the marginal zone, though many pores appear to run radially in the marginal area of the carapace when observed from the lateral side with a light microscope'. One may conclude that in some podocopids the so called marginal pores are in fact wrongly identified. The stratigraphic record of ostracods gives clear evidence that the contact margin between the two valves has been a zone of considerable evolutionary innovation. Increasingly, workers on Palaeozoic assemblages are recognising a wealth of structural detail in the calcified inner lamella and it is now established that the lack of a duplicature is not a determinant of the 'palaeocopid' condition (Gramm, 1988; Schallreuter, 1988). In *Manawa* and *Puncia* the upper surfaces of the carapace are pierced by evenly-spaced, small, simple sensillia or 'normal' pores. The sole[1] of the manawan valve

FIG. 2. Scale bar = 200 µm unless otherwise stated. A–E, incomplete ontogenetic sequence for *Puncia* sp.A. Cavalli Islands, New Zealand, 17 metres. Note progressive reduction in sub-dorsal protuberance towards adulthood. F, *Coronakirkbya fimbriata* juvenile paratype, Lower Permian, West Texas. USNM 118486. Scale bar = 300 µm. G, *Puncia* sp.B. Cavalli Islands, New Zealand, 17 metres. Juvenile? Compare and contrast sub-dorsal nodes with Figs B and H. Scale bar = 100 µm. H, *Puncia novaezealandica* Cavalli Islands, New Zealand, 17 metres. Note sub-dorsal spines. Scale bar = 100 µm. I, *Promanawa exposita* Upper Cretaceous erratic, Insel Rügen, Jasmund, Germany. Scale bar = 100 µm. J, *Puncia levis* Upper Cretaceous erratic, Insel Rügen, Jasmund, Germany. Scale bar = 100 µm.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displays an inner (close to the contact margin) and outer row of pores from which moderately long sensory setae exit (Figs 3C, 4F). A single row of between 12–15 equivalent pores and setae may be found on the proximal edge of the upper surface of the sole (Fig. 3A). Examination of the carapace of *Puncia* between the frill and the contact zone clearly indicates that the manawan pore pattern is repeated in this genus (Fig. 4A, C).

Significantly, the outermost row of setae on the ventral (when the carapace is gaping) surface of the frill are extremely long (equal to the total width of the frill in most cases). The flexibility of these setae (Fig. 4A) suggests a sensory role within the cavity created by the frill and the substrate, rather than one associated with the lateral extremities of the frill. Clearly, as the carapace gape is increased the distance between the contact margin (and therefore the animal) and the substrate is reduced to a point where such setae would no longer drape; in fact during ambulatory excursions it is likely that they are drawn across the substrate. If the punciids are capable of dispersal by floatation, it seems likely that the animal would then assume a passive/defensive role, i.e. the carapace would be closed; during such times extreme setal length in an area surrounding the carapace opening would obviously be advantageous.

Details of pore types and their distribution for Palaeozoic ostracods remain scanty, although pores have been used as stable 'landmarks' in a recent study of evolutionary change in species of *Amphissites* from the Lower Carboniferous of Australia and Upper Caroniferous of Texas (Jones, 1988). From my examination of micrographs of *Coronakirkbya fimbriata* I see no evidence of pore exits similar to those found on the underside of the punciid frill (Fig. 4A). In all instances, however, specimen/detector angles were not optimal for such a search. One row of assumed pore exits (Fig. 4D) does clearly duplicate that found on *Puncia* close to the contact margin (Fig. 4C). Because of their position close to the contact margin/sole, these may be considered analogues of 'modern' podocopid marginal pores which penetrate the carapace between the outer lamella and the duplicature. There is some evidence to suggest that the oldest 'ostracods' (see discussion Swanson, 1989a) were also open-gaped with pore exits concentrated on the carapace sole in a fashion similar to that exhibited by *Manawa*. The setal arrangement in *Puncia* therefore could represent an evolutionary intermediate step appropriate to a wide-gaped ostracod, in which a domiciliar 'early warning' system is afforded by the frill and extremely long setae. In extant benthic podocopid ostracods, because of their vertical orientation, carapace shape and narrow gape, the greatest concentration of the longest and most diverse sensory receptors (marginal pores and their setae) occur around the valve periphery near the contact margin.

LOBES

In both the Kirkbyacea and the Punciidae some representatives carry externally near their dorsal margins structures ranging from 'lobes' (used advisedly since Jaanusson, 1957 considered lobes as external expressions of internal relief) as in *Aurikirkbya* and *Coronakirkbya* to bulbs, ridges and spines, as in *Puncia* (Figs 2 E, G, H). An incomplete developmental sequence for *Puncia* sp. A (Figs 2A – E) clearly illustrates the progressive reduction in relief of two perforated, mid-dorsal, admarginal ridges. Although equivalent hollows are found on the interior of the valves, they are poor reflections of the external condition, especially in juvenile valves. Structural duplicates (for which subsurface and internal carapace detail is not available) in the Kirbyacea show a similar developmental pattern through ontogeny. In species of *Puncia*, the shape of these admarginal lobes is extremely variable; elongate, bulbous and spinose forms all occurring in the New Zealand assemblage (Figs

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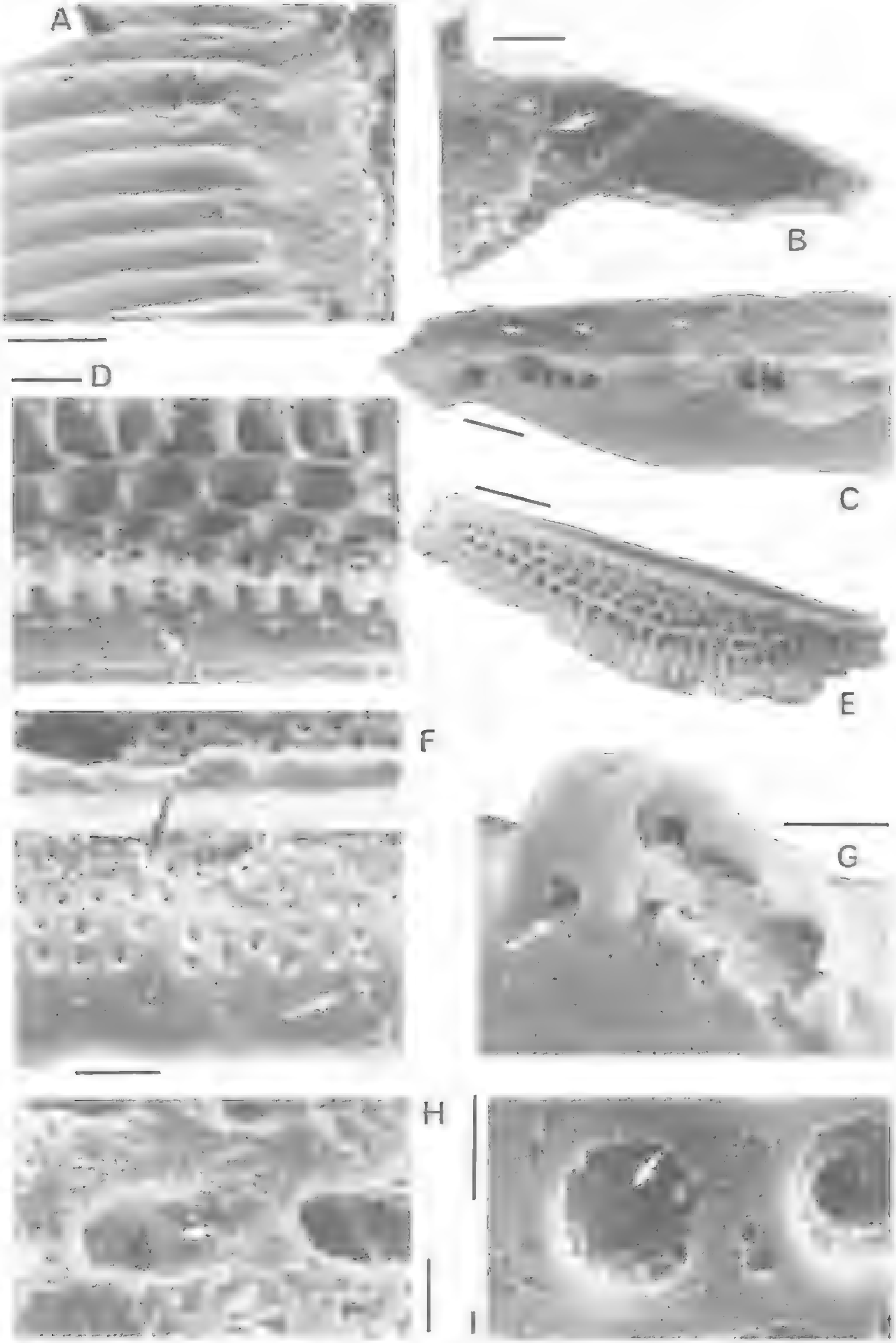
[1] Examination of the contact margin to determine the existence of a duplicature and its relation to the outer lamella have not been undertaken. Note however the structural blue-print for the sole is established with the carapace of the nauplius.

FIG. 3. Scale bar = 100 μm unless otherwise stated. A, *Manawa tryphena* Cavalli Islands, New Zealand, 8 metres. B, *Manawa staceyi* Cavalli Islands, New Zealand, 17 metres. Entire carapace in life position. C, *Manawa staceyi* Cavalli Islands, New Zealand, 17 metres. Entire carapace in life position inverted to expose soft anatomy. D, *Manawa staceyi* Cavalli Islands, 17 metres. Nauplius. Note slight bending of carapace. E, *Manawa staceyi* Cavalli Islands, 17 metres. Naupliar carapace. Arrow indicates double-walled nature of sole. F, *Manawa staceyi* Cavalli Islands, 17 metres. Metanaupliar carapace. G, *Melopetasus syltensis* Ordovician, Isle of Sylt, North Sea. Geologisch - Paläontologisches Institut der Universität Hamburg (GPIH 2233). Oblique view of "larval" carapace. H, Vertical view, specimen as for 3G.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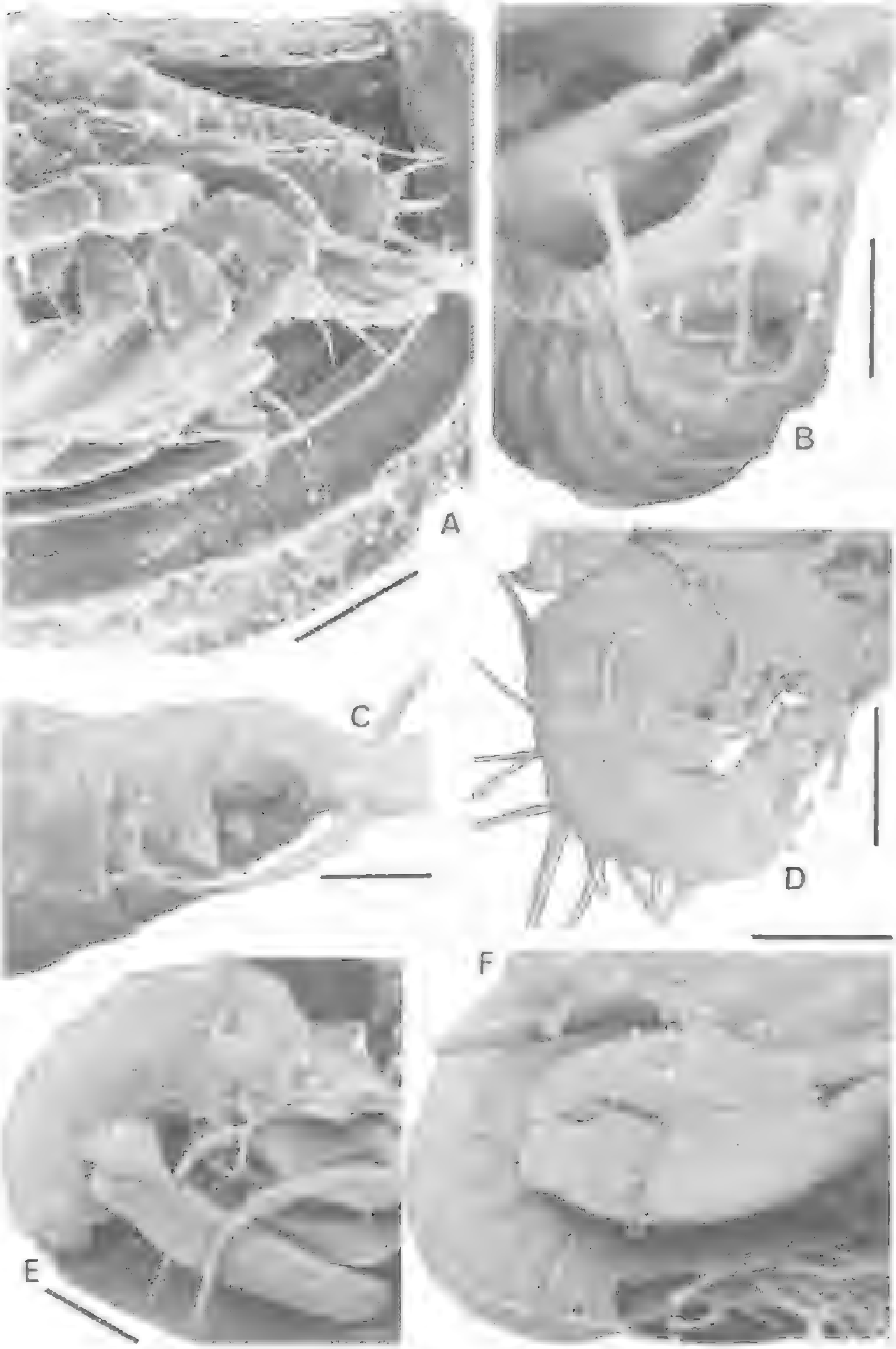
2A; 3G, H). Alternatively, in *Manawa* (Fig. 3A, B), *Promanawa* (Fig. 2I) and *Puncia* (Fig. 2J) lobate surface-swellings may occur in zones equivalent to L1 and L3 on paleocopids. Functionally, the more compact and defined ridges, knobs and spines remain a mystery. The fact that their surface expression is more pronounced earlier in ontogeny suggests some form of larval aid, noting that the subsurface detail in adults has not been investigated. Shape does not appear to influence the basic pattern of the components making up the larval admarginal 'lobe'. The dome or roof is always smooth and, unlike the rest of the carapace, unperforated; the lobal floor has a rough texture which suggests the epicuticle envelopes the entire structure. Lastly, the basal periphery of the lobe is interrupted by a number of portals in which the carapace perforations are organised in a roughly semi-circular pattern (Fig. 4G).

INTERNAL STRUCTURE

Earlier (Swanson, 1989a), I gave an indication that the internal structure of the punciid carapace also warranted further investigation. In both *Manawa* and *Puncia*, numerous, small (2–5µm) 'ducts' perforate the carapace wall perpendicular to the external surface, excluding lobes and frills or their equivalents (Fig. 4B,I; Swanson, 1989a, pl.2, fig.10). In benthic podocopid ostracods, the calcified portion of the carapace consists of a reticulate chitin fabric the interstices of which are filled with fine crystals of calcium carbonate; in those ostracods (e.g. pelagic myodocopids) for which flexibility and/or low weight seem a priority a lamellar chitin structure similar to that found in decapod Crustacea occurs (Bate and East, 1972, 1975). The carapace of most podocopid ostracods is also pierced by small 'normal' pores which display an enormous variety of form. Generally, such structures provide (a) exits for sensory setae and (b) accommodation for basal accessories of such setae. Both *Manawa* and *Puncia* do have normal pore exits but these are easily distinguished from the perforations presently under discussion (Swanson, 1989a, figs 2, 3, 9, 10; Fig. 4F, I) by the fact that the latter do not have setae. They may be densely-packed, simple, vertical tubules (*Puncia*, Fig. 4A, B, G) or larger countersunk forms in which the external rim is either papillate (*Manawa staceyi*, Swanson, 1989a, figs 3, 5) or spinose (*Manawa tryphena*, Swanson, 1989a, fig. 2). Both manawan types of duct are extremely complex internally with 'epicuticular' lining forming 2–3 continuous, membraneous bridges across each duct.

Studies of the calcified portions of the ostracod carapace clearly indicate that such structures are an economic solution to an architectural problem. 'The carapace is impregnated with massive layers of calcite during the molting and consequent growth process (unlike phyllopods and cladocerans). The result is a heavily armoured animal. There have existed through geologic time as many as twenty to thirty thousand species, all representing experiments in carapace design. As unlikely as the basic body plan may seem, it has obviously been successful' (Benson, 1981). As could be anticipated, therefore, the carapace of benthic ostracods is internally coherent with few breaks (normal pores) interrupting that continuity and often with external beams and ridges providing additional strength at a

FIG. 4. A, *Puncia* sp.A. Cavalli Islands, New Zealand 17 metres. Internal surface of frill (left = ventral) showing pore exit and seta (arrowed). Scale bar = 20 µm. B, *Puncia* sp.A. Cavalli Islands, New Zealand, 17 metres. Longitudinal section of frill showing exposed chamber and septa (upper surface = ventral). Note break is slightly oblique therefore top of next chamber also exposed. Arrow indicates 'calcareous' membrane which closes the domicilum to the frill. Note also imperfect calcification of frill at distal (right hand) extremity. Scale bar = 20 µm. C, *Puncia* sp.A. Cavalli Islands, New Zealand, 17 metres. Frill and external ventral periphery of domicilium. Note pore exists and setae (arrowed) below carapace sole. D, *Coronakirkbya fimbriata* Lower permian, West Texas. USNM 118488. Ventral periphery of domicilium showing assumed pore exists (arrowed). Scale bar = 30 µm. E, *Coronakirkbya fimbriata* Lower Permian, West Texas. USNM 118488. Ventral view of entire carapace, contact margin at top of picture. Scale bar = 300 µm. F, *Manawa staceyi* Cavalli Islands, New Zealand, 17 metres. Contact zone or sole of left valve showing two rows of pores and associated setae. Scale bar = 20 µm. G, *Puncia* sp.A. Cavalli Islands, New Zealand, 17 metres. Subdorsal protuberance. Note carapace perforations continue under portal (arrow) and contrasting texture of external carapace surface and protuberance floor. Scale bar = 20 µm. H, *Aurikirkbya wordensis* Middle Permian, West Texas, USNM 110232a. Partial view of surface reticulation. "Membranous" closure (partial) at base of each reticulation arrowed. Scale bar = 60 µm. I, *Manawa staceyi* Cavalli Islands, New Zealand, 17 metres. Note "equivalent" partial closure of one reticulation (arrowed). Scale bar = 4 µm.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minimum cost physiologically (Sylvester-Bradley and Benson, 1971, figs 1–3; Bate and East, 1972, fig. 2; Okada, 1982, text-figs 1, 16).

Why have the punciids taken the development of carapace perforations to such extremes? One possible answer lies in the unique gait of the animal. Whilst walking, both valves are carried aloft and extended, supported by relatively thin and poorly chitinised cephalic and thoracic appendages. I have already indicated that a pivotal, side to side rocking motion for *Manawa staceyi* as it walks (Swanson, 1989a) would suggest that the weight loss, resulting from a densely perforated valve, provides a partial solution to some locomotory problems. The relatively high density of perforations in *Manawa* may be used also as additional evidence to indicate the value of the frill of *Puncia* as a buoyant balancing aid. Almost all Kirkbyacea present a punctate pattern externally which duplicates that described for the punciids. Whether these negative carapace features penetrate the entire thickness of the carapace wall in the Palaeozoic forms is unknown.

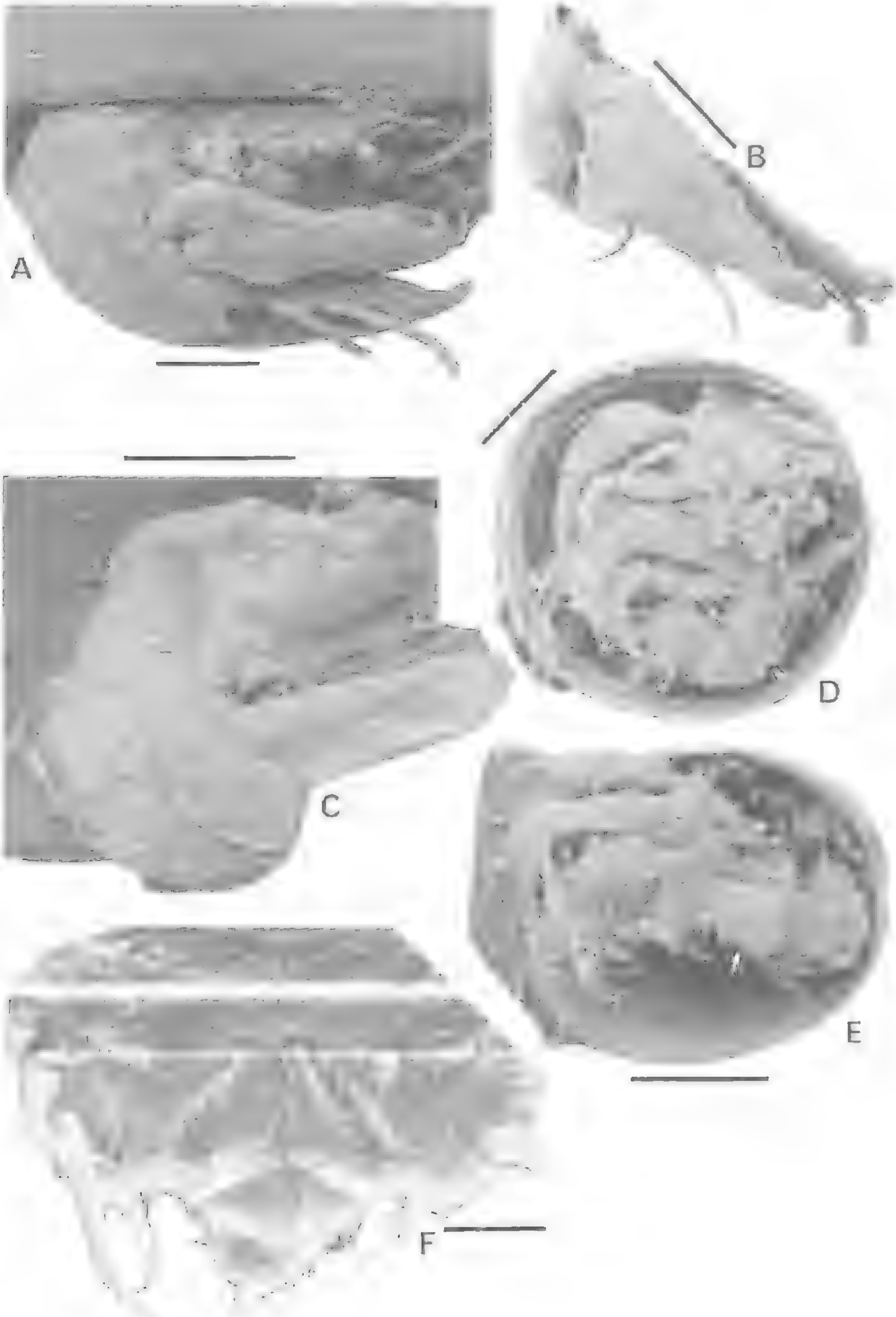
In some kirkbyids, however, the internal expression of the reticulum (if it exists) could be masked by a very thin 'calcified' membrane which may represent an extension of the inner lamella (H. Kozur, pers. comm.). Such a membraneous layer is commonly encountered in specimens of punciid ostracod and although extremely thin and transparent is sufficiently electron dense to obscure structural detail below (Swanson, 1989a, fig. 14, top right hand third of micrograph). Becker (1989) has also described subsurface closures of puncta in the kirkbyid *Aurikirkbya wordensis* which parallel those found in *Manawa* (Fig. 4H, I). I am unaware of the existence of equivalent structures in other extant ostracods.

SOFT ANATOMY

It is not my intention in this paper to discuss homologisation of manawan appendage segments, but detailed histological and scanning electron microscope examinations of their development through ontogeny are proceeding. One must acknowledge that whatever the resulting interpretation it will inevitably not meet with universal acceptance. 'Although the terms exopodite, endopodite, epipodite and the like are applied to ostracode limbs by various authors (not always harmoniously) in fact it is very difficult to homologise the individual parts of ostracode limbs with those of other Crustacea' (Maddocks, 1982). Previously, I suggested that the punciids have only three cephalic appendages (antennule, antenna and mandible) and four pediform thoracic legs. This condition (the possession of four thoracic segments) had also been proposed for Cambrian bradoriid ostracods (McKenzie and Jones, 1979). This is clearly at odds with the generally accepted limb/tagma formula for ostracods. 'It seems clear that the first four limbs belong to the cephalon and the last two to the thorax, but the fifth limb has been claimed for both' (Maddocks, 1982).

Anderson (1965, 1967) acknowledged that embryological studies of post-mandibular segment formation is of little value in assessing phylogenetic affinities amongst non-branchiopods because the possibility of paraphyletic derivation can never be excluded. Equivalent studies may prove useful in some areas of punciid biology (segmental origin of limbs) and phylogeny. The fundamental difficulty associated with the concept of a specific group of limbs allocated to specific tagma is how does one prove it and to what end? In most Crustacea, the mesoderm of the post-naupliar region even in its earliest stages gives evidence of differentiation into somite rudiments of post-maxillulary segments; i.e., differentiation of some mesodermal tissue into cellular clumps from which thoracic elements are derived is initiated during the naupliar stage. Consequently, it would be difficult to divide such a developmental sequence when it is effectively a continuum.

FIG. 5. Scale bar = 100 µm unless otherwise stated. A, *Manawa staceyi* Cavalli Islands, New Zealand, 17 metres. Posterior of body (male) including thoracic/abdominal elements and right valve. Scale bar = 40 µm. B, *Manawa staceyi* Cavalli Islands, New Zealand, 17 metres. Ventral oblique view of abdominal segments and furca. Anal flap arrowed. Scale bar = 20 µm. C, *Cytherella* sp.A. West Coast South Island, New Zealand 500 metres. Posterior-most abdominal segments and furca (male). Note anal flap and faecal pellet (arrowed). Scale bar = 40 µm. D, *Cytherella* sp.B. Off Kaikoura, South Island, New Zealand, 380 metres. Trunk showing segmentation and genital lobe, gravid female. E, *Cytherella* sp.B. Off Kaikoura, South Island, New Zealand, 380 metres. Trunk showing abdominal and thoracic (incomplete) segmentation and hemipenes, male. F, *Cytherella* sp.C. West Coast South Island, New Zealand, 910 metres. Ventral oblique view of furca, trunk and hemipene.


A
B
C
D
E
F

In terms of 'phylogenetic' studies, Anderson (1965, 1967) gave indication of a embryological developmental progression from that of the cephalocarids in which 'mesodermal segmentation precedes ectodermal segmentation in the primitive manner'; to the derived malacostracan condition in which 8 mesoteloblasts '....bud off successive rows of 8 cells which form the somite rudiments of individual segments, and a corresponding row of ectoteloblasts bud off ectoderm which lies outside the somite rows and becomes segmentally associated with them'. Embryological studies of 'primitive' and 'modern' ostracods may give some indication of polarity within Anderson's sequence and as a result confirm or refine present concepts of ostracod phylogeny and relationships with other Crustacea.

ABDOMEN

Ostracoda are generally regarded as non-segmented and cephalised (McKenzie, 1983), and their trunk and abdominal reduction, as a result of segmental loss, is the most extreme of any crustacean. Nevertheless, after a study of the chitino-skeleton of several living taxa, Schultz (1976) concluded that ostracods had abdominal segmentation earlier in their phylogeny. On the basis of this evidence and the possession of other 'primitive' limb and carapace characters, at least five groups of ostracods are repeatedly utilised as providing examples of bauplans (acknowledging such constructions only as indications of what is possible) from which 'modern' ostracods may have evolved. I have excluded the Polycopidae from this discussion because they have fewer segments in the trunk (Fig. 6D, E). Saipanettid ostracods will be discussed only in a general sense because detailed electron micrographs were not available for study. As noted by Maddocks (1982), Schulz considered *Saipanetta* to represent a phylogenetic intermediate between the ancestral Platycopina and descendant Podocopina. On the basis of the carapace detail Schallreuter and Jones (1984) included the Punciocopa (Kirkbyacea and Punciacea) in the extant Platycopa. Discussion of morphological aspects of the abdomen of the platycopid *Cytherella* is warranted because superficially, at least, it appears to resemble that described for *Manawa staceyi* (Swanson, 1989a).

The trunk of male cytherellids is dominated by paired hemipenes which are attached to the body on or near segments 5 to 7 (Figs 5E, F, 6A – C). Chitinous skeletal elements of the abdomen are produced anteriorly to provide what may be structural support for each hemipenis and genital lobe (in females). From the present study the precise origin of each hemipenis could not be determined; what is encouraging however is (a) its structural variation between taxa and (b) the existence of 'segmentation' (Fig. 5E, F) indicating a potential source of important taxonomic and phylogenetic information. The anlage of the hemipenis appears quite early in ontogeny (A-3 or A-4), as does abdominal segmentation (Fig. 6C).

Kornicker (1975) argued that the position of the furca relative to the anus should be given more emphasis in ostracod classification. Schulz (1976) figured the cytherellid trunk as being composed of ten segments, a telson and furca; according to him the anus was located between the tenth segment and the telson, dorsal to the furca. Kornicker (1975) also placed the cytherellid anus dorsal to the furca but behind the telson. Scanning electron microscope examination of a number of critical-point dried specimens of *Cytherella* confirms Kornicker's view. The anus occurs after the last full segment and an anal flap is present (Fig. 5C). Also of interest is the presence of a 'faecal' pellet composed of coccolith remains which may indicate that cytherellids operate as 'collectors' (Kornicker, 1975: 41) rather than as efficient benthic filterers (Cannon, 1933). Note also that the posterior-most (in life position) ventral elements of the furca may also function as 'housekeeping' accessories (Fig. 5F).

Members of the Punciidae also have ten trunk segments with a poorly understood 'reproductive' element between segments 5 and 7. Both *Cytherella* and *Manawa* carry paired lamel-

FIG. 6. Scale bar = 100 μm unless otherwise stated. A, *Cytherella* sp.D. West Coast South Island, New Zealand 320 metres. Ventral oblique view of male abdominal segments, furca and hemipenes. B, *Cytherella* sp.E. West Coast South Island, New Zealand 320 metres. Hemipenes and abdomen (male). C, *Cytherella* sp.B. Off Kaikoura, South Island, New Zealand 380 metres. Trunk and hemipene of juvenile male. D, *Polycope* sp. Inside Crayfish Reef, Kaikoura, South Island, New Zealand, 14 metres. Entire adult enclosed in right valve; abdominal segments arrowed. E, *Polycope* sp. Inside Crayfish Reef, Kaikoura, South Island, New Zealand, 14 metres. Entire juvenile enclosed in right valve; abdominal segments arrowed. F, *Manawa staceyi* Cavalli Islands, New Zealand, 17 metres. Metanauplius 3, anal segment and furcal anlage. Scale bar = 10 μm.

liform furcae, the setae of which differ numerically (more in *Cytherella*) and structurally (derived ?). The anal position in *Manawa* duplicates that found in *Cytherella* although in the former the anal flap occurs after the 'telson' (Fig. 5B). Both Kornicker (1975) and Schulz (1976) indicated that in *Saipanetta* the anus exits dorsal to the furca. This was seen by Kornicker (1975) as confirmation of the podocopid status of the saipanettids, since members of the Myodocopida (with which *Saipanetta* has some furcal similarity) have the anus ventral to the furca. The fact that *Saipanetta* has six trunk segments and a telson shows that its abdominal condition is more derived than that of platycopid or punciid ostracods but less than that of most extant ostracods.

Abdominal evidence for a direct punciid-platycopid link (Schallreuter and Jones, 1984) is not convincing; when combined with substantial contrasts in anatomy and carapace structure it seems unlikely. I suggest that segmentation of the trunk and abdominal configuration as found in *Cytherella* and *Manawa* is the plesiomorphic condition for ostracods. This does not exclude the possibility that both lineages developed independently.

CONCLUSIONS

1. As indicated by Hornibrook (1949) and confirmed by the present study, the carapace of the Punciidae is unlike that found on any other extant ostracods.
2. On the basis of detailed comparison of a number of key carapace characters it is concluded that punciid ostracods are the only living representatives of the predominantly Palaeozoic Kirkbyacea.
3. Similarities in abdominal soft anatomy of platycopid and punciid ostracods probably reflect the plesiomorphic ostracodal condition; contrasts in other aspects of soft anatomy and the carapace suggest that the inclusion of Punciocopa in the extant order Platycopa is unwarranted.
4. The position of some Cambrian bradoriid 'ostracodes' in which the abdomen is reduced or absent should now be reassessed.

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